ward; the following are farther south.) Thomas County: Purdum, 1901, *Baker*. Dawson County: 1943, *Kiener*, Arthur County: 1943, *Kiener*. 2.) The eastern face of the Black Hills of southwestern South Dakota in Custer, Pennington, Lawrence, and Meade counties: Jim Creek (T. 2 N., R. 5 E.) 1913, *Setzer;* Bear Butte Creek (T. 4 N., R. 4 E.), 1919, *Murdoch;* Castle Creek, 1924, *Over;* Castle Creek near Deerfield, 1928, *McIntosh;* near Merritt, 1924, *Over;* Squaw Creek, 12 miles above Game Lodge, 1926, *McIntosh;* Sylvan Lake, 1926, *McIntosh;* Custer, 1928, *McIntosh*. 3.) Estes Park, northern Colorado. Larimer County: Estes Park, elevation 7500 feet, 1933, 1934, *Ernest C. Smith* (seven collections). 4.) The Pikes Peak area in east-central Colorado. Teller County: east of Divide, 1935, *J. H. Christ*. El Paso County: Black Forest, 1935, *J. H. Christ*.

The sandhills area of Nebraska-South Dakota, and the Black Hills area of South Dakota, lie some 300 to 400 miles west-southwest of the margin of the continuous eastern distribution. The two mountain localities in Colorado are about 100 miles apart and 300 to 350 miles southwest of the Nebraska and South Dakota areas and therefore some 600 to 700 miles southwest of the margin of continuous distribution.

In the case of *Salix serissima*, there are four isolated and distant localities of discontinuous distribution, in three States. In the case of *S. petiolaris*, there are two relatively extensive areas and two isolated mountain localities of such distribution, also in three different States.

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SEED GERMINATION IN GILIA CAPITATA AND ITS RELATIVES

Verne Grant

The discovery that seeds of *Gilia capitata* Douglas (Polemoniaceae) collected from a recently burned hillside in the California Coast Ranges germinated twice as well as seeds from an unburned site in the same immediate area posed both the practical problem: how to obtain the highest percentage of germination from the seeds available for experimentation; and the theoretical problem: whether fire is a factor in the distribution of *Gilia capitata*. The observation, again, that the closely allied races, *G. chamissonis* Greene and *G. staminea* Greene, are confined in nature to pure sands on the California coast and in the San Joaquin Valley raised the question whether the distribution of these entities is related to the germination requirements of their seeds or the tolerances of their seedlings at establishment. Numerous germination tests, in which temperature, substrate, and other factors were varied, were then undertaken.

Like many other herbaceous elements in the California flora, *Gilia capitata* and its allies germinate with the first heavy rains of the fall. The spiracles of the seed coat imbibe water immediately upon being wetted and form a gelatinous sheath about the seed. Within a few days the embryo emerges and the pair of green cotyledons is soon raised above the ground. The seedlings with their first true leaves pass the winter from November until February or March in a semi-dormant condition; upon the first warm temperatures of spring they then resume growth.

Methods

Seed collections in bulk and by families (individual seed parents) were made from the following strains of *Gilia capitata* and its close relatives in California: *G. capitata* from an open hillside swept by a surface fire during the year of seed collection, Mayacama Mountains, Napa County; *G. capitata* from the same hillside in a local oak grove not touched by the fire; *G. capitata* from Tomales Bay, Marin County; *G capitata* from Hatchet Mountain, Shasta County; *G. chamissonis* from sand dunes on Point Reyes Peninsula, Marin County; *G. chamissionis* from sand hills of San Francisco; *G. staminea* from sand hills near Antioch, Contra Costa County; *G. staminea* from Mather, Tuolumne County. (The foregoing entities are being treated by the author as subspecies of the polytypic species *Gilia capitata* in a monographic study which will shortly be in press.) In addition, seeds from experimental cultures and artificial hybridizations were obtained, as outlined in a subsequent paragraph.

Seed treatment was varied as follows:

1. Controls. Untreated seeds were planted in sand flats in the greenhouse.

2. Scarification. The seed coats were scratched between two pieces of sandpaper in a petri dish.

3. Stratification at constant temperatures. Flats containing the seeds were watered and stored immediately in a cold room for two, four, or six weeks at 2.5° C. or 5.0° C.

4. Stratification at alternating temperatures. The flats were stratified overnight at 5° C. and brought out into a warm room during the day. This process was continued for two, four, or six weeks.

5. Restratification. The stratified flats, after being removed to the greenhouse for germination, were subsequently returned to the cold room for a second treatment with cold temperatures, followed by a second period in the greenhouse (Quick, 1943).

6. Heating of seeds at 150° C. The seeds were placed in open petri dishes in an electric oven at 150° C. for 5 minutes, then planted in sand in the greenhouse and watered.

7. Heating of seeds at 750° C. The seeds were put in a small wire screen box which was then fastened to the end of a stick. A flash fire of excelsior was built in a fire place. At the height of the blaze the wire box containing the seeds was passed through the flames for three seconds.

8. Planting of whole capsules. The capsules of *G. staminea* and *G. chamissonis* are dehiscent and contain numerous, small seeds which are normally sprinkled out of the open ends with the swaying of the peduncles in the wind. The capsules of *G. capitata* in the Coast Ranges are by contrast indehiscent, 1–3-seeded, and tend to disarticulate and fall out of the calyx at maturity. In an effort to determine the possible adaptive significance of this latter combination of characters, undehisced capsules of *G. capitata* from the Mayacama Mountains were planted in sand in the greenhouse. The germination percentage was calculated on the basis of the estimated number of seeds present.

9. Stratification of whole capsules at 2.5° C.

10. Heating of whole capsules at 150° C.

11. Heating of whole capsules at 750° C.

12. Heating of whole capsules at 750° C. followed by immediate stratification at 2.5° C. in wet sand.

13. Washing the seeds in frequent changes of distilled water before sowing.

14. Sand in 6 inch pots in greenhouse. This was a control for the following three variations in type of substrate.

15. Autoclaved sand in greenhouse.

16. Adobe-clay in 6 inch pots in greenhouse.

17. Adobe-clay in the experimental field, Berkeley. Since the same parent soil was used here as in the greenhouse pots, the chief variable was soil temperature, which in spring of course was much lower outdoors.

The effect of genetic factors on seed germination was inferred in two ways:

The germination percentage of F_1 hybrid seeds was compared with the germination percentage for the parental entities. The seeds of both the species and the hybrids were harvested from plants growing under the same greenhouse conditions, and were planted and stratified side by side in the same flats.

Ten seeds from each of twenty-one randomly selected individual plants in the Mayacama colony of *G. capitata* were sown and their germination percentages were determined. This process was repeated for the seven strains under examination. The variance between strains was then compared with the variance between families.

Environmental Effects on Germination

The principal results are shown in Table 1, where the numbers heading the various columns correspond to the paragraph num-

TABLE 1. THE EFFECTS OF VARIOUS ENVIRONMENTAL FACTORS ON SEED GERMINATION IN GILIA CAPITATA AND ITS RELATIVES. (The numbers heading the columns correspond to the paragraph numbers under "Methods.")

Treatment	1		3,4		8,9		6,10		7,11,12		14		16		17	
	Controls		2.5-5.0°C		Whole capsules		150°C		750°C		Sand, green-house		Clay, green-house		Clay, field	
Strain	% Germination	no. Seeds	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.
Mayacama Mts., unburned area	8	200	32	740	1	275	0	50	0	179						
Mayacama Mts., burned area	24	50	61	948			0	97			2	50	4	50	14	50
Tomales Bay	45	100	88	427												
Pt. Reyes	25	100	77	654							4	50	4	50	10	50
San Francisco			77	293												
Antioch			52	420							8	50	14	50	8	50
Mather	40	100	46	536												
Hatchet Mt.			31	366												

bers for methods of treatment; in certain columns the data for the two different treatments have been combined. The strain of *G. capitata* from the burned area in the Coast Ranges germinates much better than the strain away from the burn in both the controls and the stratified lots. Stratification increases the percentage and uniformity of germination in all strains. No significant difference was found between constant and alternating temperatures, between 2.5° C. and 5.0° C., or between two and six weeks stratification. After six weeks the seeds germinated in the cold room. *Gilia staminea* from four thousand feet elevation in the Sierra Nevada (Mather) appears not to require stratification any more than the lowland strains (cf. also Mirov, 1936).

When whole capsules of Coast Range *G. capitata* are sown, instead of thrashed seeds, the result is zero per cent germination without stratification, and one per cent (of the estimated number of seeds) germination with stratification.

The exposure of either naked seeds or whole capsules to 150° C., a temperature which some grass seeds withstand (Sampson, 1944), evidently injured the seeds for no germination at all was obtained. The temperatures of a flash fire are likewise deleterious to the seeds of *G. capitata* with or without the protective covering of the capsule.

As regards the effects of the substrate, *G. staminea* and *G. chamissonis,* both restricted to pure sands in nature, germinate and become established as well on clay-adobe as on sand.

Treatments which had no apparent effect were: use of autoclaved sand, washing the seeds with distilled water, scarification, and restratification. These experimental treatments have been omitted from Table 1. *Gilia capitata* differs in respect to the results of restratification from certain species of *Phacelia,* in which restratification is effective (Quick, 1947).

Table 2. Frequency Distribution of Germination Percentages by Families in Seven Strains of Gilia capitata and its Close Relatives. (About 21 Families Per Strain and About Ten Seeds Per Family.)

Strain	0%	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Mayacama Mts., burned area			2	1	1	4	4	1	6	1	1
Tomales Bay					1			1	3	6	11
Pt. Reyes			1		1		5	2	6	6	1
San Francisco			1	1		2	1	3	5	4	3
Antioch		3	2	2	2	3	5	2	1	1	1
Mather	5	1		2	2	1	3	1	4		
Hatchet Mt.	3	2	5	3	3	2	1	1	1	1	

Genotypic Effects on Germination

The germination of seeds from different seed parents (viz. families) of the same population is shown in Table 2. Undoubtedly there is great variation from family to family, as an examination of the germination percentages for the Mayacama strain of *G. capitata* will reveal. Analysis of the variance showed that there is significantly more variation between strains than within strains, but that the variation from family to family within one strain is much greater than would be expected if due to chance alone. The non-random variation in germination between families of one strain may be due to differential environmental influences on the seed parents, to genotypic differences between seed parents, or to both sets of factors. Similarly the differences in germination between strains may be due to differences in environment, genotype, or both.

Crosses between four of the strains would seem to indicate that germination behavior has a hereditary basis. The germination of the F_1 seeds is not intermediate with respect to that of the entities, but in most cases is better than either parental type (fig. 1). Whether this is to be taken as a manifestation of that debated quantity known as hybrid vigor depends on one's definition of hybrid vigor. The data suggest at least that germination percentage is in part under genotypic control.

Discussion

Gilia staminea and *G. chamissonis* are inhabitants of relatively loose sandy soils in nature. In cultivation the plants will flower and fruit in pure sand watered only with tap water; they thrive much better, however, if transplanted to richer soils. Germina-

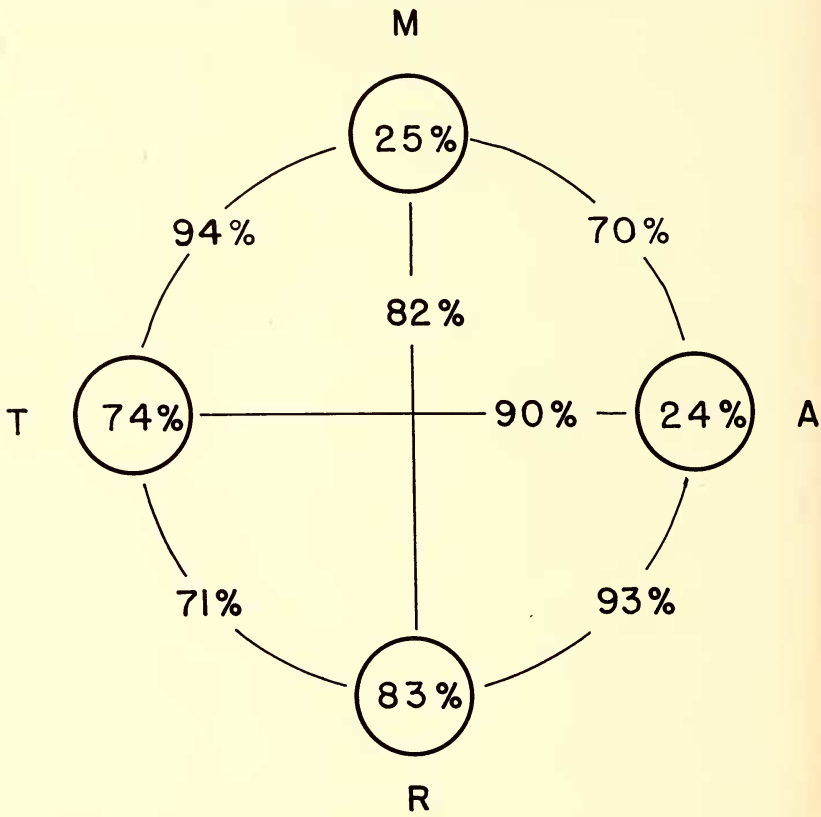

Fig. 1. Percentages of seed germination in four parental strains of *Gilia capitata* and its close relatives, and their F_1 hybrids. The parental strains are represented as circles. M, Mayacama Mountains; A, Antioch; R, Point Reyes Peninsula; T, Tomales Bay. In each case, percentages are based on 140 to 280 seeds.

tion tests show that the seeds germinate and the seedlings become established on adobe-clay in Berkeley under both field and greenhouse conditions. These facts taken together with the observation that *G. staminea* and *G. chamissonis* do not successfully withstand the competition of more aggressive species, either in nature or in the garden, suggest that the micro-distribution of *G. staminea* and *G. chamissonis* within their distributional areas may be the resultant of a tolerance for impoverished habitats and an intolerance of competition.

Gilia capitata occurs on sunny hillsides in the Coast Ranges. It is one of the commonest plants in clearings following a fire. Germination tests indicate that the seeds of *G. capitata* do not endure even moderately high temperatures. Certain other facts about this plant provide a clue as to the possible reasons for its abundance on burned areas; both field observations and garden tests show that *G. capitata* does not tolerate either deep shade or dense growth. With its annual life cycle and its low mineral requirements it is, like *G. staminea* and *G. chamissonis,* primarily a pioneering species on open habitats. Fire, by removing a more mature vegetation, returns the habitat to a stage suitable for colonization by *G. capitata.*

Summary

1. There is marked variation between and within populations of *Gilia capitata* Dougl. and its allies as to percentage of seed germination. Some of this variation is genotypic; some of it is environmentally conditioned.

2. The seeds of both highland and lowland strains of *G. capitata* and its close relatives germinate relatively well when planted in moist sand without previous treatment. Stratification for two weeks at temperatures just above freezing improves germination. Restratification and scarification are ineffective. Brief exposure of the naked seeds or undehisced capsules of Coast Range *G. capitata* to temperatures of 150° C. or higher completely inhibits germination.

3. The micro-distribution of *G. capitata* and its allies is discussed in the light of the germination tests and some other observations. The confinement of *G. staminea* and *G. chamissonis* to sandy soils in nature, and the abundance of *G. capitata* in clearings following fires, may best be explained by regarding these plants as pioneers fitted for open habitats, but not tolerating the conditions of competition and shade in closed communities.

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Literature Cited

Grant, V. 1949. A genetic and systematic analysis of the Gilia capitata complex. Unpublished Ph. D. thesis, Univ. of Calif., Berkeley.

Mirov, N. T. 1936. Germination behavior of some California plants. Ecology 17: 667–672.

Quick, C. R. 1943. Certain methods of forcing the germination of seeds. Jour. Calif. Hort. Soc. 4: 95–102.

———. 1947. Germination of Phacelia seeds. Madroño 9: 17–20.

Sampson, A. W. 1944. Plant succession on burned chaparral lands in northern California. Univ. Calif. Agr. Exp. Station Bull. 685.